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Experimental manipulations of the arthropod, nematode and earthworm communities in a North American tallgrass prairie

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With 2 figures

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1. Introduction

Biocides have been widely used to evaluate the impacts of soil fauna on decomposition and mineralization processes (e.g. Whitkamp & Crossley 1966; Edwards *et al.* 1969; Parker *et al.* 1984). Biocides have also been used to assess the importance of root-feeding nematodes on net plant productivity (Smolik 1977; Ingham & Detling, unpublished). Findings from studies using biocides are complicated by unmeasured effects of chemicals on non-target organisms, and these non-target organisms may subsequently affect variables under study such as mineralization or plant production. However, a large literature is available on the response of many invertebrate groups and microbes to various biocides (Andrén & Steen 1978; Ingham & Coleman 1984). The availability of this information, along with careful qualification of results, makes the experimental manipulation of fauna with chemicals a viable, albeit imprecise, procedure to evaluate interactions among the biota.

An insecticide was applied to foliage and an insecticide-nematicide was applied to the soil surface of a North American tallgrass prairie site in an attempt to manipulate population densities of invertebrate consumers. The objectives of this study included (1) measurement of impacts of the dominant root herbivores, June beetle larvae (*Phyllophaga* spp.; Scarabaeidae) on plant root biomass and production; (2) to evaluate nematode and earthworm response to the chemicals and to correlate changes in these groups with changes in living or dead plant mass, and (3) to test if differences in densities of aboveground invertebrate consumer groups directly or indirectly affected population densities of the belowground groups. The last question resulted from an observation by Seastedt (1985) that moderate aboveground herbivory appears to increase population densities of soil nematodes and certain arthropod groups.

2. Study site and methods

Research was conducted on the Konza Prairie Research Natural Area, a 3,487 hectare site located about 20 km south of Manhattan, Kansas, in the Flint Hills of northeastern Kansas. Dominant vegetation on this site is characterized by tallgrass prairie species such as big bluestem (*Andropogon gerardii* Vitman, 1792), Indian grass [*Sorghastrum nutans* (L) Nash, 1903], and switchgrass (*Panicum virgatum* L., 1753). A general description of the vegetation and soil fauna of the tallgrass prairie is presented in Risser *et al.* (1981). The earthworms of Konza Prairie have been studied by James (1982), while soil arthropod trophic composition and population densities have been reported by Seastedt (1984a, b). A list of nematode species has also been compiled for a native prairie site 44 km north of the Konza Prairie (Orr 1965).

The study was conducted on an upland site with shallow (40 cm to bedrock) silty-clay soil (Typic Natrustolls). This site was burned in early April of 1983 and 1984 to remove standing dead plant vegetation and litter. This management procedure is common in the tallgrass prairie region to maxi-

mize plant productivity (e.g. KNAPP 1984); however, we employed the procedure primarily to simplify sampling and quantification of vegetation. This area was then divided into 96 6 m × 6 m plots Chemical treatment was applied to the innermost 4 m × 4 m square, while sampling was restricted to the innermost 3 m × 3 m area. A two-factor factorial design was used to create 24 replicates of the following four treatments: **(1)** untreated, **(2)** foliage and soil surface invertebrates reduced, **(3)** soil invertebrates reduced, and **(4)** both above- and belowground invertebrates reduced. A carbamate insecticide (carbaryl, Sevin®, Union Carbide, Co.) was used to reduce invertebrate population densities in the foliage and soil surface. This chemical is reported to photo-oxidize rapidly, and has no residual effects (KUHR & DOROUGH 1977). Thus, the carbamate should have had no direct effect on true soil invertebrates. An organophosphate (isofenphos, Oftanol®, Mobay Chem. Co.) was used to reduce soil invertebrates. This organophosphate was selected because of its known ability to control white grubs (Scarabaeidae) in turf grass. The carbamate treatments were applied weekly during the growing season, while the organophosphate was applied once in May of 1983 and in May and June of 1984. A greenhouse study using isecticide-treated and untreated big bluestem indicated that neither chemical produced a stimulatory or toxic effect to the plants. A small quantity (ca $0.20\ g \cdot m^{-2} \cdot a^{-1}$)[1]) of liquid urea was applied to control and isofenphos plots to match the input of nitrogen from the carbamate.

Aboveground plant standing crops were measured by clipping 0.1 m^2 quadrats on each of the 96 plots. Plant material was sorted into grasses and forbs, dried at 60 °C to constant mass, and weighed. Root biomass was measured by obtaining two, 5 cm diameter by 30 cm deep cores on each of 48 plots (12 per treatment) and washing the roots from the soil with an apparatus described by SMUCKER *et al.* (1982). Rhizome standing crops were obtained by digging 0.1 m^2 by 30 cm deep soil monoliths and hand sorting the soil for all rhizome fragments. All belowground plant materials were sorted into living and dead categories based on color and condition of the stele, dried and weighed. Subsamples of all belowground materials were ashed, and mass is reported on an ash-free basis.

Samples used to obtain rhizomes were also used to obtain estimates of macroarthropod population densities and biomass. All visible arthropods (with the exception of ants and termites) were hand-sorted from the 0.1 m^2 by 30 cm deep soil monoliths and separated into broad trophic groups, dried and weighed. The trophic composition of the prairie macroarthropods has been described by SEASTED (1984a) and SEASTEDT *et al.* (in press). In general, June beetle larvae or white grubs (mostly *Phyllophaga* spp.; Scarabaeidae) are the dominant root-chewing insects, while cicada nymphs (Cicadidae) are the dominant, large sucking root-feeders. Many of the grubs have two or three year life cycles (HAYES 1925), while the cicadas have life cycles of two or more years (BEAMER 1928). The dominant soil arthropod predators include centipedes (Chilopoda), robber fly (Asilidae), horse fly (Tabanidae) and carabid beetle larvae. Millipedes (Diplopoda) compose most of the arthropod detritivore biomass. Mass of macroarthropods was obtained after drying specimens at 70 °C for 24 h.

Earthworms were collected by hand in 1984 along with the other materials from the soil monoliths. Earthworms and their cocoons were killed in 70% ethanol in the field and transferred to 4% formalin. Identifications of adult lumbricids were made according to REYNOLDS (1977). Most specimens of Lumbricidae were *Aporrectodea turgida* EISEN, 1873. Adults of *Diplocardia* spp. (Acanthodrilidae) were identified to species following GATES (1977). Wet mass was converted to dry mass with species specific regression equations obtained by JAMES (1983).

Microarthropods were sampled only once in the autumn of 1983 using a high-gradient extraction procedure described by SEASTEDT (1984b). Aboveground arthropods were sampled at regular intervals with a vacuum sampler. The results will be presented elsewhere; however, the insecticide did reduce aboveground arthropod densities (E. W. EVANS, unpublished).

Nematode densities were estimated from soil samples collected at approximately monthly intervals from June through December in 1983 and June through September in 1984. Two 5 cm diameter soil cores were removed to a depth of 20 cm from six plots of each treatment on each date. Nematodes were extracted from 100 cm^3 subsamples using a modification of the Christie-Perry Technique (CHRISTIE & PERRY, 1951). Recovered nematodes were identified to genus or higher taxon using morphological characters discernible at 100 × magnification, counted, and assigned to trophic groups as described by FRECKMAN (1982) (obligate herbivores, facultative herbivores/fungivores, microbivores, predators, and omnivores; Table 1). Extraction efficiency, measured by multiple extractions of samples from non-treated plots and examination of residues collected on a 38 μm screen, was approximately 30% for the dominant nematode genera present. Data analysis and presentation, however, is based on actual numbers of nematodes extracted.

3. Results

3.1. Plant and detritus standing crops

A general trend towards increased biomass and necromass of plant tissues occurred during the two-year study (Table 2). An increase in plant production is well documented for native tallgrass prairie that has had standing dead and litter removed in the spring by

[1]) The symbol a (for the Latin annus) is used here instead of yr (year).

Table 1. Trophic and taxonomic groupings of nematodes used in data comparisons

Trophic Level	Taxonomic Order	Dominant Genera
Obligate Herbivores (32)[a]	Tylenchida (95)	*Gracilacus, Helicotylenchus, Paratylenchus, Tylenchorhynchus*
	Dorylaimida (5)	*Xiphinema*
Facultative Herbivores/ Fungivores (45)	Tylenchida (91)	*Aphelenchus, Aphelenchoides, Tylenchus*
	Dorylaimida (9)	*Diphtherophora, Tylencholaimellus, Tylencholaimus*
Microbivores (16)	Rhabditida (74)	*Acrobeles, Cephalobus, Eucephalobus*
	Monhysterida (20)	*Monhystera*
	Araeolaimida (6)	*Plectus*
Predators (3)	Enoplida (89)	*Prismatolaimus, Tripyla*
	Mononchida (11)	*Mononchus*
Omnivores (5)	Dorylaimida (93)	*Aporcelaimellus, Eudorylaimus*
	Rhabditida (7)	*Mesodiplogaster*

[a]) Figure in parentheses indicates the average percent composition of each grouping from non-treated control plots throughout 1983—1984.

Table 2. Amounts of live and dead plant parts, 1983—1984, in $g \cdot m^{-2}$

Material	1983		1984	
	June	Oct.	June	Oct.
Foliage[1]	201 (12.1)	381 (12.6)	192 (6.0)	444 (12.2)
Live Rhizomes	168 (7.8)	186 (11.8)	206 (10.7)	219 (10.8)
Live Roots	376 (26.0)	439 (29.2)	491 (18.5)	600 (23.4)
Dead Rhizomes	81 (7.9)	96 (7.7)	42 (4.0)	73 (5.3)
Dead Roots	278 (19.3)	384 (14.8)	531 (22.4)	496 (19.2)

[1]) Foliage represents production from the current year only.

Note: Values are means and standard errors of 96 samples per date (foliage) or 48 samples per date (roots and rhizomes).

Table 3. Population densities and biomass of soil macroarthropods, 1983—1984

Artropod group	Control		Isofenphos		Carbaryl		Both chemicals	
	$no \cdot m^{-2}$	$g \cdot m^{-2}$	$no \cdot m^{-2}$	$g \cdot m^{-2}$	$no \cdot m^{-2}$	$g \cdot m^{-2}$	$no \cdot m^{-2}$	$g \cdot m^{-2}$
Herbivores **(total)**	**29.1**	**.39**	**32.2**	**.42**	**36.7**	**.84***	**26.0**	**.31**
	(4.2)	(.08)	(5.3)	(.10)	(4.1)	(.17)	(4.2)	(.08)
June Beetle Larvae	5.7	.23	7.9	.26	11.0	.63*	3.8	.15
	(1.2)	(.07)	(1.9)	(.09)	(2.4)	(.18)	(1.0)	(.06)
Cicada Nymphs	4.3	.10	3.1	.05	5.6	.12	2.3	.08
	(1.2)	(.03)	(1.0)	(.01)	(1.3)	(.03)	(0.9)	(.03)
Detritivores **(total)**	**9.1**	**.17**	**10.2**	**.16**	**10.4**	**.29**	**18.3**	**.20**
	(2.2)	(.04)	(3.2)	(.05)	(2.2)	(.13)	(6.5)	(.06)
Millipedes	4.7	.10	6.9	.09	5.0	.12	14.6	.14
	(1.4)	(.02)	(2.9)	(.03)	(1.6)	(.04)	(6.3)	(.04)
Predators **(total)**	**14.2**	**.17**	**9.8**	**.16**	**10.6**	**.11**	**13.1**	**.13**
	(1.9)	(.04)	(1.8)	(.05)	(1.3)	(.03)	(2.0)	(.04)
Centipedes	4.9	.02	2.9	.01	5.8	.04	5.0	.03
	(0.9)	(.01)	(0.8)	(.00)	(1.0)	(.01)	(.1)	(.02)
Total arthropods	**52.4**	**.73**	**53.2**	**.74**	**57.7**	**1.24***	**57.4**	**.63**
	(6.1)	(.06)	(6.7)	(.12)	(5.3)	(.23)	(8.6)	(.09)

*Significantly different from controls (ANOVA $p < .05$).

Note: Data are means and standard errors of 48 samples per treatment.

Table 4. Analysis of variance for factors influencing nematode densities

Source	degrees of freedom	Obligate Herbivores	F-Value[1] Faculative Herbivores/ Fungivores	Microbivores	Predators	Omnivores	Total
Date (D)	8	4.44**	18.09**	2.96**	8.21**	5.91**	**15.03****
Carbaryl (C)	1	0.05	0.29	0.04	0.12	1.33	**0.02**
Isofenphos (I)	1	0.01	11.09**	33.33**	21.57**	0.10	**4.96***
D×C	8	0.68	0.81	0.69	0.63	0.60	**0.87**
D×I	8	1.09	1.00	1.10	2.07*	0.56	**1.44**
C×I	1	1.22	0.43	2.63	0.81	0.26	**0.19**
D×C×I	8	0.79	0.81	1.15	0.29	2.43*	**0.75**
error	155						

[1] Variance attributed to variable after all other variables entered into ANOVA. * = $p < .05$; ** = $p < .01$.

fire or raking (e.g. HADLEY & KIECKHEFER 1963). Only standing crops of dead roots were significantly affected by the isofenphos treatment during 1983 ($p < .05$). Root detritus averaged 322 $g \cdot m^{-2}$ in untreated plots, and 367 $g \cdot m^{-2}$ in treated plots. Intensive sampling resulted in precise estimates of standing crops (Table 2). However, no significant differences in plant or litter mass were noted for carbaryl treatments, and no statistically significant differences among treatments were observed during the second year for any of the plant variables.

3.2. Arthropod response

A comparison of the control and carbaryl plots with the isofenphos and both chemical plots indicated that isofenphos was moderately effective in reducing the biomass of soil arthropods. However, a strong interaction between the carbaryl and the isofenphos was reported in the analysis of variance procedure. Means obtained from the isofenphos and carbaryl plots were therefore individually compared with the controls, and these data (Table 3) indicate that only results from the carbaryl plots differed from those of the controls. June beetle larvae, total herbivore biomass and total biomass in the carbaryl plots were greater than those observed in the controls, while no significant differences existed among the control, isofenphos, or isofenphos plus carbaryl plots. While this result was unexpected (and somewhat disappointing given that isofenphos was labeled for white grubs), the chemical manipulation still produced a different level of belowground arthropod herbivores in one of the treatments. Numbers and biomass of the dominant arthropod herbivore group in the carbaryl plots was approximately double that in other treatments, but this difference failed to result in changes in plant standing crops of roots.

Microarthropod population densities estimated in autumn 1983 showed no statistically significant effects for any treatment ($p > .05$ for all sources, $n = 32$). Densities averaged 48,700, 40,900, 43,100 and 39,300 individuals in the top 5 cm of litter and soil per m^2 in control, carbaryl, isofenphos, and both chemical plots, respectively. These population densities are not atypical for annually burned tallgrass prairie (SEASTEDT 1984b).

3.3. Nematode response

Nematode trophic groups were differentially affected by isofenphos (Fig. 1; Table 4). Fungivorous, microbivorous, and predaceous nematode populations were significantly reduced an average of 23, 34, and 42%, respectively ($p < .05$). Obligate herbivores and omnivores, however were not consistently affected. Carbaryl did not have a measurable effect on nematode populations.

Nematode densities exhibited large seasonal variation with similar trends for all trophic groupings except the microbivores, which were less affected by sampling date (Fig. 1).

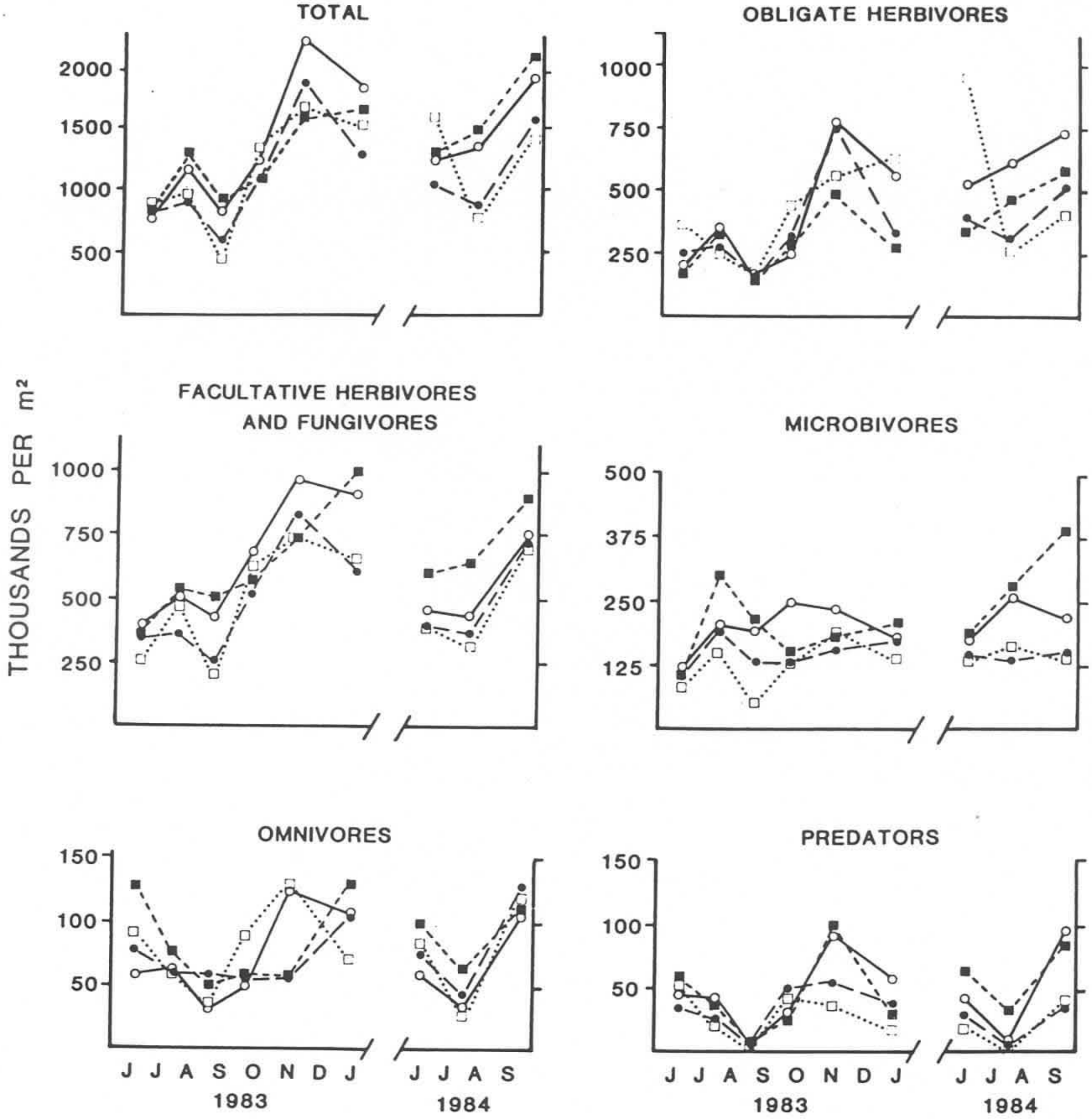

Fig. 1. Nematode population densities on control (○), carbamate (■), organophosphate (●) and both chemical (□) plots sampled over a dates in 1983 and 1984.

Highest densities occurred when soil water was relatively abundant on the prairie, while lowest densities were observed during periods of drought. However, YEATES (1982) has demonstrated that annual population cycles of nematodes are often better correlated with plant production than with soil moisture. A more detailed analysis of the effects of various edaphic and production factors on the observed variations in nematode population densities will be published separately.

3.4. Earthworm response

Aporrectodea turgida and *Diplocardia* spp. responded differently to the two pesticides (Fig. 2). The European earthworm, *A. turgida*, increased in biomass on the plots treated with carbaryl or with carbaryl and isofenphos, while the native North American species (dominated by the species *Diplocardia smithii*) exhibited increased population densities and biomass on the isophenophos treated plots and on the carbaryl and isofenphos plots (Table 5).

Table 5. Analysis of variance for factors influencing earthworm biomass and population densities

Source	degrees of freedom	F-Value[1]		Total
		Diplocardia spp.	*Aporrectodea turgida*	
Population densities				
Date (D)	1	0.72	2.09	**1.82**
Carbaryl (C)	1	0.55	1.61	**0.00**
Isofenphos (I)	1	6.93**	0.17	**7.51****
D × C	1	0.58	1.22	**0.19**
D × I	1	0.05	0.40	**0.02**
C × I	1	0.47	0.41	**0.03**
D × C × I	1	0.52	0.53	**0.61**
error	88			
Biomass				
Date (D)	1	3.60	2.77	**7.27****
Carbaryl (C)	1	2.50	5.32*	**1.15**
Isofenphos (I)	1	6.95**	0.48	**1.18**
D × C	1	0.03	1.21	**1.08**
D × I	1	0.12	0.04	**0.00**
C × I	1	0.35	0.31	**0.08**
S × C × I	1	0.62	0.95	**1.77**
error	88			

[1] Variance attributed to variable after all other variables entered into ANOVA. * = $p < .05$; ** = $p < .01$.

4. Discussion

The application of isofenphos at recommended rates did not have a measurable affect on the target arthropods. Since most of the grubs and all of the cicadas have multiple year life cycles, effects should have been cumulative. Immigration into treated plots by lateral movement over the surface or through the soils was not studied. The fauna may have remained protected by remaining in deeper soil horizons, below the zone of effective penetration of the insecticide.

The modest declines or increases observed in nematode and arthropod herbivore and detritivore densities did not result in any measurable change in net primary productivity. We conclude that net primary productivity of the tallgrass prairie is not particularly sensitive to changes in the nominal population densities of belowground consumers. Plants do not appear to make major changes in energy allocation patterns when modest shifts in herbivore intensities occur (e.g. Janzen 1983). Somewhat surprisingly, the detritus-based system appeared more sensitive to our chemical manipulations, with an increase in the standing crops of dead roots observed in 1983, and an increase in earthworm population densities observed in 1984. The 1983 increase in dead roots was correlated with reductions in population densities of free-living microbivore/fungivore-feeding nematodes. Our findings are consistent with other studies showing a relationship between soil invertebrates and decomposition and mineralization of organic matter (e.g. Anderson *et al.* 1983; Parker *et al.* 1984).

Increases in population densities and biomass of earthworms in pesticide-treated soils have been reported by Griffiths *et al.* (1967) and Grigoreva (1952). These responses are usually attributed to release from arthropod predators. Ruppel & Laughlin (1977) reported that carbamate pesticides are generally toxic to earthworms, but that organophosphates have little negative effect. Our results (Fig. 2) indicated that both isofenphos and the carbaryl had either a neutral or positive effect on the earthworms. A differential effect was observed between native and introduced species. *Diplocardia* spp. increased in densities and biomass in the isofenphos-treated plots, while *Aporrectodea turgida* increased in biomass on the carbaryl-treated plots.

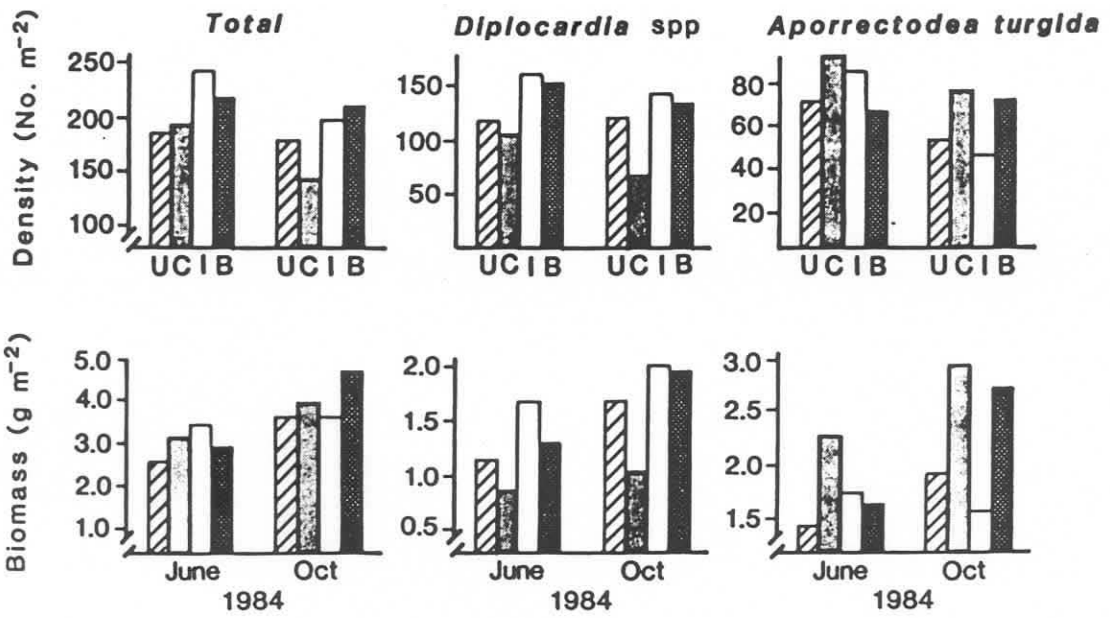

Fig. 2. Earthworm population densities and biomass on untreated (U), carbaryl (C), isofenphos (I) or both chemical (B) plots in June and October 1983.

The presence of *Aporrectodea turgida* (see EASTON (1983) and SIMS (1983) for discussion of synomyms of *A. turgida*, and *Allolobophora caliginosa* SAVIGNY 1826) has been reported to greatly increase plant productivity in grasslands (STOCKDILL 1966, 1982). Very little is known about the activities of *Diplocardia* spp. which are endemic to North America. JAMES & SEASTEDT (in press) found that *A. turgida* in tallgrass prairie is a facultative surface-feeder, and both feeds and casts on the soil surface. In contrast, the *Diplocardia* spp. appear to be deeper soil forms, and do not feed on the soil surface. Certainly the response observed in this study corroborates those findings; the surface-feeder benefited by an apparent reduction in aboveground or surface dwelling arthropods, while the true soil forms may have benefited by application of the organophosphate and a reduction in free-living nematodes. However, we cannot state the exact mechanisms responsible for these increases.

5. Summary

1. Modest changes in soil invertebrate population densities by chemical application did not affect net primary production of tallgrass prairie.
2. Modest reductions in free-living soil nematodes during the first year of the study was correlated with a 15% increase in the amount of dead root mass in the soil. No such response was observed the second year when earthworm densities had increased on these plots.
3. Free-living soil nematodes were more sensitive to organophosphate (isofenphos) application than were the plant parasitic forms.
4. Population densities of native earthworms (*Diplocardia* spp.) were enhanced by isofenphos addition. This response may have resulted from a reduction in competition and/or predation.
5. June beetle larvae (*Phyllophaga* spp.) and the introduced earthworm, *Aporrectodea turgida*, exhibited statistically significant increases in biomass in the carbaryl treated plots.
6. Overall, the detritus-detritivore subsystem appeared more sensitive to chemical manipulation than did the root-herbivore subsystem.

Zusammenfassung

Experimentelle Manipulation von Boden-Arthropoden-, Nematoden- und Lumbriciden-Gemeinschaften in einer Nord-amerikanischen Hochgras-Prairie

1. Mäßige Änderungen der Boden-Invertebraten-Besatzdichten durch Anwendung von Agrochemikalien (Bioziden) beeinflußt die Netto-Primär-Produktion der Hochgras-Prairie nicht.
2. Eine mäßige Verminderung der Zahl der freilebenden Nematoden war, während des ersten Untersuchungsjahres, mit einer 15%igen Zunahme toter Wurzelmassen korreliert. Im zweiten Jahr wurde keine solche Auswirkung beobachtet, nachdem die Dichte des Regenwurmbesatzes auf den behandelten Parzellen zugenommen hat.

3. Freilebende Boden-Nematoden waren gegenüber einer Behandlung des Bodens mit Organophosphaten (Isofenphos) empfindlicher als pflanzenparasitische Formen.
4. Infolge der Isofenphos-Anwendung waren die Besatzdichten der einheimischen Regenwürmer (*Diplocardia* spp.) erhöht. Diese Zunahme des Regenwurmbesatzes könnte die Folge einer geminderten Konkurrenz und/oder eines geringeren Feinddruckes durch Prädatoren sein.
5. Junikäfer-Larven (*Phyllophaga* spp.) und die allochtone (ursprünglich europäische) Regenwurm-Art *Aporrectodea turgida* zeigten statistisch signifikante Zunahmen der Biomassen in den mit Carbaryl behandelten Parzellen.
6. Insgesamt scheint das Detritus-Detritivora-Subsystem gegenüber bioeiden Manipulationen empfindlicher zu sein als das Wurzel-Herbivoren-Subsystem.

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Synopsis: *Original scientific paper*

SEASTEDT, T. R., T. C. TODD, & S. W. JAMES, 1987. Experimental manipulations of arthropod, nematode, and earthworm communities in a North American tallgrass prairie. Pedobiologia **30**, 9—17.

Organophosphate (isofenphos) and carbamate (carbaryl) insecticides were used in a two-factor factorial experimental design to evaluate interactions among the invertebrate fauna in a North American tallgrass prairie. Modest changes in nematode and arthropod densities did not result in any changes in plant standing crops. A small but statistically significant increase in detritus standing crops occurred during the first year in treatments that reduced nematode and arthropod densities, but this effect disappeared in the second year when densities of native earthworm species (*Diplocardia* spp.) became more abundant in these plots. A European earthworm, *Aporrectodea turgida*, also became more abundant in plots treated with carbaryl (which reduced densities of canopy arthropods), but not in plots treated with isofenphos. The earthworm response is hypothesized to be the result of release from negative interaction(s) (i.e., competition and/or predation) with the arthropods.

Key words: Tallgrass prairie, plot experiments insecticides, organophosphate, isofenphos, carbamate, carbaryl, soil fauna, interaction.